

TAXONOMIC NOTES ON WESTERN AMERICAN GENTIANACEAE¹

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In the manuscript on the Gentianaceae recently prepared for *The Jepson Manual* of the flora of California, departures from previous treatments of certain taxa require further explanation than would be feasible within the manual itself. The appropriate discussions, along with a nomenclatural combination that must be validated for use in the manual, are presented below.

THE CIRCUMSCRIPTION OF *SWERTIA*

Wood & Weaver (1982) have called the circumscription of *Swertia* L. "perhaps the most controversial in the Gentianaceae." Over the years about a dozen genera have been segregated from *Swertia* s. lat. Recent authors have generally treated the Eurasian and African representatives of this complex as one genus, but, with regard to the North American species, the status of *Frasera* Walt. remains unresolved.

Until recently the segregation of *Frasera* was rejected in most standard floras, following *Die natürlichen Pflanzenfamilien* (Gilg 1895) and St. John's (1941) monograph of *Swertia* s. lat. in North America. During the past thirty years, however, generic status for *Frasera* has gradually been gaining acceptance. This has been based in large part on unpublished studies by D.M. Post ca. 1948–1957, summarized by Hitchcock (1959) and Threadgill & Baskin (1978). *Frasera* has also been accepted in Wood & Weaver's (1982) recent discussion of generic delimitation in the Gentianaceae of the southeastern United States. My preliminary discussion of this question in 1979, in contrast, advocated the inclusion of *Frasera* in *Swertia*.

Basic chromosome numbers have been emphasized in support of generic status for *Frasera*, although a suite of morphological characters has been presented as being correlated with chromosome number. Wood & Weaver (1982) described *Frasera* as having $x = 13$, whereas "the perennial species of *Swertia* s. str. have numbers mostly based on 14." Post (paraphrased by

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Hitchcock 1959) went so far as to suggest "that *Frasera*, with a basic chromosome number of 13, is perhaps more closely related to *Gentiana* (which has a similar number) than to *Suertia*." Toyokuni (1965) expanded *Frasera* to include those Japanese species then known to have $x = 10$, essentially basing this treatment on chromosome numbers alone, but this circumscription has not been adopted by subsequent authors. Wood & Weaver (1982) commented that "this alignment is contradicted by other characters." Among the Japanese species, for example, *S. pseudochinensis* Hara, with $n = 10$, is especially similar in morphology to *S. perennis* L., the type species of the generic name *Suertia*, with $n = 14$.

Unfortunately, chromosome numbers were known for only a few species in this complex until recently. Since the papers cited above were written, chromosome counts have been published for many more species of *Suertia* s. lat. (compiled 1973–1988 in *Regnum Veg.* 90, 91, 96, *Monogr. Syst. Bot. Missouri Bot. Gard.* 5, 8, 13, 23, and *Taxon* 35, 36; see also Table 1). Also, as is often the case, a few early counts have not been substantiated by further investigations of the same species and must be considered unreliable. With chromosome numbers now known for over 40 species in this complex from all parts of its range, a much clearer picture of the distribution of chromosome numbers in *Suertia* s. lat. is now available. This picture is considerably at variance with some extrapolations made from early counts.

It is now evident that the majority of species in *Suertia* s. lat. have $x = 13$ (usually $n = 13$, occasionally $n = 26$ or 39). A smaller number of Asiatic species have $x = 10$ (usually $n = 10$; $n = 30$ in *S. tashiroi* (Maxim.) Makino). Associated with each of these groups are a few aneuploid species having one more or one fewer (in *S. paniculata* Wallich two fewer, $n = 8$) chromosomes per genome than the prevailing number. Of these, the amphi-Pacific *S. perennis* L. (including *S. cuspidata* (Maxim.) Kitigawa, *S. obtusa* Ledeb., and *S. stenopetala* (Regel & Tiling) Pissjauk., segregates seldom accorded specific rank) is the only species known to have $n = 14$ or any multiple thereof.

The generic name *Frasera* Walt. is typified by *S. caroliniensis* (Walt.) Kuntze (as *F. caroliniensis* Walt.), a species of eastern North America with $n = 39$. Wood & Weaver (1982) followed all of the earlier interpretations of *Frasera* except Toyokuni's in restricting this genus to North American species, implicitly assigning to it all species of *Suertia* s. lat. native to this continent except *S. perennis*. They characterized *Frasera* morphologically by: cauline leaf bases weakly connate, not decurrent (free, long-decurrent in *Suertia*); flowers always tetramerous with one nectary pit per corolla lobe (*Suertia* usually with pentamerous flowers and two nectary pits per lobe,

some species either with tetramerous flowers or with solitary nectaries); and a distinct filiform style (stigma sessile or nearly so in *Suertia*). Threadgill & Baskin (1978), following Post, listed axis type, general anatomy, phyllotaxis, nodal anatomy, number of flower parts, and presence of a style as morphological features by which *Frasera* and *Suertia* s. str. were differentiated.

Suertia bimaculata (Sieb. & Zucc.) C.B. Clarke and *S. swertiopsis* Makino, both of Japan, correspond ideally to Wood & Weaver's concept of *Suertia* s. str. in morphology, being perennial and having striate internodes, pentamerous corollas with paired nectaries, and, in *S. bimaculata*, a sessile stigma, yet both have $x = 13$. *Suertia bimaculata* has the same number, $n = 13$, as the taxon called *Frasera pabutusensis* Reveal (probably best included in *S. albicaulis* (Griseb.) Kuntze), an ideal "*Frasera*" with tetramerous corollas and single nectaries. Pentamerous corollas with paired nectaries also occur in species with $x = 10$, e.g. *S. japonica* (Schult.) Makino and *S. pseudochinensis* Hara, but so does the combination of tetramery and single glands, as in *S. tashiroi*.

The significance of the number of nectaries per corolla lobe can clearly be discounted. In western North America, *S. radiata* (Kellogg) Kuntze (*F. speciosa* Douglas ex Griseb.) most closely resembles *S. caroliniensis* in general aspect, life history, stem structure, phyllotaxy, foliar and floral morphology, and chromosome number (both $n = 39$). It has consistently been placed in *Frasera* by all who have accepted the genus, but it has paired nectaries. In Asia both single and paired nectaries can be found associated with both tetramerous and pentamerous flowers. Paired nectaries — i.e., the actual groups of nectariferous cells at the base of a pit — may open into a single pit, as in the Asiatic species *S. alata* (D. Don) C.B. Clarke, *S. angustifolia* Buch.-Ham. ex D. Don, *S. nervosa* (G. Don) C.B. Clarke, and *S. ciliata* (D. Don ex G. Don) B.L. Burtt; or the nectariferous zone may be w-shaped, as in the American species *S. neglecta* (H.M. Hall) Jeps. Conversely, many species have solitary nectaries opening into pits with u-shaped or notched openings. Even within a single species or on an individual plant, as in the Asiatic *S. atrovioleacea* H. Sm., there may be various degrees of fusion of the nectary pits.

Pentamery is not constant in *S. perennis*; individual specimens have been found to be variable in this study, with tetramerous flowers being quite common. Occasional tetramerous flowers were also noted on specimens of *S. bimaculata* and *S. japonica*, and have been reported in other species that normally have pentamerous flowers. Styler differences between *S. perennis* and "*Frasera*" are a matter of relative length rather than being qualitative. In this study, distinct albeit slender styles were observed in *S. perennis*,

TABLE 1. Partial list of *Suertia* species for which chromosome numbers have been published (see text for sources), with floral characters and phyllotaxy.

SPECIES	RANGE	N	COROLLA LOBES	PITS/ LOBE	PHYLLOTAXY
<i>S. alata</i> (D. Don) C. B. Clarke	Asia	13	4	1	opposite
<i>S. albicaulis</i> (Griseb.) Kuntze (<i>S. pabutensis</i> (Reveal) J. Pringle)	N. Am.	13	4	1	opposite
<i>S. angustifolia</i> Buch - Ham. ex D. Don	Asia	13	4	1	opposite
<i>S. badomei</i> C. B. Clarke	Asia	13	4	1	opposite
<i>S. bimaculata</i> (Sieb. & Zucc.) C. B. Clark	Asia	13	5	2	opposite
<i>S. chirayita</i> (Roxb. ex Fleming) Karsten	Asia	13	4	2	opposite
<i>S. cordata</i> (G. Don) C. B. Clarke	Asia	13	5	1	opposite
<i>S. corymbosa</i> (Griseb.) C. B. Clarke	Asia	13	4	1	opposite
<i>S. densifolia</i> (Griseb.) Kashyapa	Asia	13	4	1	opposite
<i>S. lurida</i> (D. Don ex G. Don) C. B. Clarke	Asia	13	4	2	opposite
<i>S. nervosa</i> (G. Don) C. B. Clarke	Asia	13	4	1	opposite
<i>S. petiolata</i> Royle ex D. Don	Asia	13	5	2	opposite
<i>S. speciosa</i> (D. Don) C. B. Clarke	Asia	13	5	2	opposite
<i>S. thomsonii</i> C. B. Clarke	Asia	13	5	2	opposite
<i>S. trichotoma</i> (Wight) C. B. Clarke	Asia	13	4	1	opposite
<i>S. suerttopsis</i> Makino	Asia	26	5	2	opposite
<i>S. carolinensis</i> (Walt.) Kuntze	N. Am.	39	4	1	whorled
<i>S. radiata</i> (Kellogg) Kuntze	N. Am.	39	4	2	whorled
<i>S. perennis</i> L.	N. Am., Eurasia	14	5 or 4	2	opposite or alt.
<i>S. ciliata</i> (D. Don ex G. Don) B. L. Burtt (<i>S. purpurascens</i> (D. Don) C. B. Clarke)	Asia	10	5	1	opposite
<i>S. diluta</i> (Turcz.) Benth. & Hook. fil. (<i>S. tosaensis</i> Makino)	Asia	10	5	2	opposite

<i>S. japonica</i> (Schult.) Makino	Asia	10	5	2	opposite
<i>S. minor</i> (Griseb.) Knohl.	Asia	10	4	2	opposite
<i>S. pseudochinensis</i> Hara	Asia	10	5	2	opposite
<i>S. tashiroi</i> (Maxim.) Makino	Asia	30	4	1	opposite
<i>S. tetragona</i> (Edgew.) C.B. Clarke	Asia	9	5	2	opposite
<i>S. paniculata</i> Wallich	Asia	8	5	1	opposite
			or 4		

scarcely exceeded by those of some "*Frasera*" species. *Swertia swertiopsis*, which as noted above is otherwise an ideal "*Swertia*" in morphology, has a relatively long, slender style. Sessile stigmas do occur in *Swertia* s. lat., but are variously combined with pentamery and tetramery, single and paired nectaries, and $x = 10$ and 13.

Both whorled and opposite leaves occur within North American "*Frasera*" and within several other species-groups. Connate leaf bases, although prominent in *S. caroliniensis* and *S. radiata*, are not present in some opposite-leaved North American species, at least at the upper nodes. Post's (1958) published study of nodal anatomy, specifically the number of gaps in the stele associated with leaf traces at successive nodes, divided the North American species into five groups. The difference in nodal anatomy between his group V, which comprised *S. perennis* alone, and group IV of "*Frasera*," does not appear significantly greater than the difference between groups I and IV of "*Frasera*." Its citation by later authors as supporting a generic division was based on a supposed correlation with basic chromosome numbers and morphological features. No Eurasian or African species were included in Post's study.

The striking difference in aspect between the familiar *S. caroliniensis* and *S. radiata*, which have tall, stout, hollow stems, and *S. perennis*, which is of lower stature with slender, solid stems, cannot be used to support the segregation of *Frasera* from *Swertia* (unless *Frasera* were to be restricted to the two stout-stemmed species). Most North American species have slender, solid stems and narrower leaves, and are of much lower stature than the two hollow-stemmed hexaploids. The basic inflorescence type throughout *Swertia* s. lat. is a thyse or verticillaster, comprising a determinate (usually elongate) axis bearing opposite or whorled branches that terminate in dichasial cymules. Within North American "*Frasera*" there is considerable diversity in total inflorescence size, height at which the lowest inflorescence branches are produced, and length of internodes in the inflorescence — as much within "*Frasera*" as between "*Frasera*" and residual *Swertia*

species. Conversely, within residual *Suertia* there is extreme diversity in general aspect and in inflorescence branching. Many Asiatic species are similar in these respects to some of the slender-stemmed "*Frasera*" species of North America, including some species with narrow, crowded inflorescences and others with diffuse inflorescences (see Pringle 1979 for examples). The Asiatic and Indonesian taxa also include, however, such highly dissimilar species as *S. dichotoma* L., with small flowers and slender, decumbent stems giving the plants a chickweed-like aspect (or, as the old name *Anagallidium* Griseb. for a generic segregate suggests, an *Anagallis*-like aspect); *S. zeylanica* (Griseb.) C.B. Clarke, with a flat-topped inflorescence; *S. acaulis* H. Sm., with a greatly reduced inflorescence axis, the long pedicels appearing to arise from the caudex; *S. pubescens* Franch., with each flower subtended by a pair of large, ovate bracts; and other species respectively resembling *Gentianella* and *Deianira* species in general aspect. These diverse habits show no correlation with the floral characters discussed above.

Nilsson (1967) found that all species of *Suertia* s. lat. that he studied had basically similar pollen, the grains being separate, prolate, and tricolpate, with the exine striato-reticulate. He did find that all North American species of *Suertia* s. lat. except *S. perennis* shared an exine structure unusual for the genus, with finer striations and more closely spaced baculae than those of most other species. Such pollen, however, was also found in one Japanese and two Himalayan species. Of these, *S. japonica* has $n = 10$, pentamerous corollas, and paired nectaries; and *S. handeliana* H. Sm. (chromosome number unknown) combines the "*Frasera*" characters of tetramerous flowers and single nectaries with the sessile style attributed to *Suertia* s. str. (The third species has not been described, at least not under the unpublished name by which it was known to Nilsson.) Among the Asiatic species there was considerable diversity in exine structure. Nilsson retained the broad concept of *Suertia*.

Differences in xanthone chemistry have been alleged to support the segregation of *Frasera*, but the early studies (see Threadgill & Baskin 1978 for citations) dealt with too few species to reveal patterns within *Suertia* s. lat. Later investigations of the oxygen-substitution positions of xanthones in the Gentianaceae by Jossang et al. (1973) included nine species of *Suertia* s. lat., the North American species being represented by *S. albicaulis* and *S. caroliniensis*. Species represented by more than one specimen were generally variable in xanthone chemistry. Substitution at position 2 was restricted to *S. albicaulis* and *S. caroliniensis* among the species studied, but was not found in all specimens of either of these species. At least one sample of *S. caroliniensis* was identical in xanthone chemistry to samples of *S. perennis* as

well as *S. chirayita* (Roxb. ex Fleming) Karsten ($n = 10$, lobes 4, nectary 1), *S. diluta* (Turcz.) Benth. & Hook. fil. var. *tosaensis* (Makino) Hara (*S. tosaensis* Makino; $n = 10$, lobes 5, nectaries 2), and *S. swertiopsis*. Their study, therefore, does not provide support for generic status for *Frasera*.

In summary, data now available show that the morphological characters associated with "*Frasera*" are restricted neither to North American species nor to species with $x = 13$, nor are they consistently correlated with one another in their occurrence. Conversely, rather than differing in basic chromosome number, most species of *Suertia* s. str. and "*Frasera*" have the same basic number. Although, as indicated particularly by Nilsson's studies, the North American species of *Suertia* exclusive of *S. perennis* may have a monophyletic origin, this group does not appear to have differentiated from its Asiatic relatives sufficiently to justify its recognition as a genus or even to permit the characterization of such a genus. No suite of correlated characters nor, as far as evidence is available, even one character reliably separates "*Frasera*" from *Suertia*. The same criteria by which Wood & Weaver rejected the segregation of Japanese taxa as *Frasera* species and restored them to *Suertia* (above) also preclude the segregation of the North American species. Therefore *Suertia* will be retained in the broad sense in *The Jepson Manual*.

THE STATUS OF *SWERTIA UMPQUAENSIS*

According to Peck & Applegate (1941), their *Frasera umpquaensis* was much like *F. fastigiata* (Pursh) Heller (*Suertia fastigiata* Pursh) in general aspect and had "quite similar foveae" (nectary pits), "differing in the setae and in the characteristics of the calyx." The former reference was evidently to "setae" (trichomes in the present paper) on the corolla in the "area below the [nectary] pit" similar to those surrounding the opening of the pit. Such trichomes would be designated corona trichomes in the terminology now prevalent for floral descriptions in this genus. Peck & Applegate may have assumed that their presence constituted a distinction because Card's (1931) "Revision of the genus *Frasera*" lacked any mention of such trichomes in his description of *F. fastigiata* or any representation of them in his illustration of corolla details (although the corona trichomes of other species were shown). Peck & Applegate described the calyx lobes of *F. umpquaensis* as being "linear to lance-linear, somewhat unequal, 9–12 mm long," whereas Card described those of *F. fastigiata* as "somewhat subulate, 2 cm long."

Actually, *S. fastigiata* does have a corona of trichomes near the base of the corolla, as is clearly shown in Abrams' (1951) and Hitchcock's (1959) illustrations of this species. Hitchcock described the calyx lobes of *F. fasti-*

giata as lanceolate, 5–13 mm long, although as illustrated they could be termed linear. Supposed differences in calyx-lobe shape appear merely to reflect different authors' interpretations of descriptive terms.

The only distinction between *S. fastigiata* and *S. umpquaensis* cited by Abrams was in the apex of the corolla lobes, described in *S. umpquaensis* as being narrowed "rather abruptly at the apex to a slender apiculation with 1-few minute teeth." Such characters tend to be variable within species of *Suertia*, and their aspect may be affected by maturity and by preparation of specimens. An "apiculation" appears in Hitchcock's illustration of the corolla of *F. fastigiata*.

In the present study, comparison of specimens from California identified as *S.* or *F. umpquaensis* with specimens from the Blue Mountains of Oregon and from Idaho identified as *S.* or *F. fastigiata* disclosed no differences by which two taxa could be distinguished.

A NEW COMBINATION IN *GENTIANA*

Extreme forms of *Gentiana newberryi* A. Gray s. lat., treated as *G. newberryi* s. str. and *G. tiogana* Heller by Mason (1960), are connected by too many intermediates to permit their interpretation as two ordinarily well-differentiated species that occasionally hybridize where their ranges overlap. Intermediate forms outnumber specimens of *G. newberryi* s. str. and prevail to the virtual exclusion of either extreme in some regions (note distribution of "hybrids" as mapped by Mason 1960). Nevertheless, the relatively tall plants with blue corollas that occur in the Klamath Ranges of California and in Oregon (*G. newberryi* sensu Mason) do appear to merit some taxonomic distinction from the more widespread "*tiogana*" plants with white or faintly blue-tinged corollas in the Sierra Nevada of California and adjacent Nevada. The following combination is therefore made:

GENTIANA NEWBERRYI A. Gray var. *TIOGANA* (Heller) J. Pringle, comb. nov. — BASIONYM: *Gentiana tiogana* Heller, Leaf. W. Bot. 2:221. 1940.

Gentiana newberryi var. *newberryi* in this concept corresponds to *G. newberryi* sensu Mason (1960). Some plants in the Cascade Ranges and the northernmost Sierra Nevada of California appear to be genuine intermediates. Most of the "hybrids" and "intermediates" of earlier identifications, however, should probably be included in var. *tiogana* as low-altitude forms.

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